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TRENDS IN POLLINATION BIOLOGY¹

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ABSTRACT

An effusion of books and articles on pollination biology has appeared recently, showing a renewed interest in this area of reproductive biology that has strong significance for the continuous evolution of seed plants. Consequently, a comprehensive review is not possible in this paper; topics have been selected and a restricted number of examples given. New findings in "classical" pollination scenarios are reported, while newer topics include the chemistry of nectar in relation to phylogeny and pollinator types. The formation of "pollination ecotypes" within species is considered but the obstructive influence of "phylogenetic constraint" on close adaptation between flower and pollinator is illustrated. Collaboration with other kinds of biologists will be important. Relevant post-pollinatory events are considered briefly. Some of the requirements for pollination study at population and ecosystem levels, including those of pollinator sharing and mimicry, are reviewed. Botanic gardens and field stations will play a prominent role in these endeavors.

Key words: pollination, nectar-chemistry, pollination-ecotypes, phylogeny, pollinator-sharing, mimicry.

INTRODUCTION

What's new in pollination biology? And what will develop?

One thing that is immediately obvious is that there has been a vast increase in attention paid to the reproductive biology of seed plants in the last two decades. This has not only involved professional biologists but also amateurs who can make natural history contributions of merit, beyond just naming the plants that they find. There has been an outpouring of journal articles that boggles the mind, but the interest that has been stirred up has led to the production of an unusual number of new books and review articles that summarize the state of the science.

RECENT LITERATURE

Books formed from collected papers at symposia on diverse aspects of pollination biology are represented by Anon. (1979), Richards (1978), Armstrong, Powell and Richards (1982), Bentley and Elias (1983), Jones and Little (1983), and Real (1983). Complete books on pollination have been produced by Meeuse and Morris (1984) and Barth (1985); both of these books are particularly well illustrated, and the latter considers the morphology, physiology, and ethology of the insects in greater detail than is usual in pollination writings. Another book with beautiful illustrations is by Dobat (1985) which reviews all that has been published on the specialized subject of pollination by bats. Faegri and Van der Pijl (1979) published a third edition of their well-known book on pollination ecology. "Pollination '82" and "Pollination '84" are reports of research in progress published at the University of Melbourne, Australia (Williams and Knox 1982, 1984). Review articles particularly dealing with pollination by insects have been

written by Kevan and Baker (1983, 1984). A chapter describing reproduction of plants in tropical rainforests (Baker, Bawa, Frankie and Opler 1983) contains pollination material and, in her book on reproductive biology, Willson (1983) provides information on prefertilization phenomena as well as a more detailed consideration of postfertilization biology.

Because of the great volume of relevant material this paper cannot be a comprehensive review, if I try to indicate where I believe that progress in pollination biology will take place in the future, I must usually pick out single examples of the various trends that appear. I want to cover these areas:

First, new findings in classic studies; then the newer types of investigation that may be introduced or expanded in the future; followed by consideration of the integration of botany and botanists with other disciplines; and competition between the plants and animals involved in pollination, leading to investigations at the level of the ecosystem. In all cases the trend is to produce quantitative data rather than anecdotal reports and there is an increasing attempt to follow observation by experiment in the elucidation of pollination problems.

NEW FINDINGS IN CLASSIC STUDIES

Yuccas and yucca moths.—I have recently reviewed the literature on the classic case of obligatory mutualism between *Yucca* plants and yucca moths (Baker 1986).

In 1872, George Engelmann and Charles V. Riley discovered the close relationship of the yucca moth now called *Tegeticula yuccasella* (Riley) and *Yucca* plants in Missouri. This relationship turned up elsewhere, too, and by the end of the second half of the twentieth century had reached a stage where there were said to be three yucca moth species with mutualistic relationships with *Yucca* plants. Two of these *Tegeticula* species were associated with only one yucca species each (*T. maculata* [Riley] on *Yucca whipplei* Torr. and *T. paradoxa* [Riley] on *Y. brevifolia* Engelm.) while all the other yuccas were believed to be pollinated by *Tegeticula yuccasella* (McKelvey 1938, 1947).

But recent research by Miles (1984) in Texas, J. Addicott (pers. comm.) in the Great Basin, and Powell (1985) in Arizona, suggest that *Tegeticula yuccasella* contains a number of cryptic species and there may be at least a race for each species of *Yucca*, although the plentiful production of hybrids by the genus *Yucca* suggests that there is some plasticity in host selection by the moths. Also it is not clear that the moths fly frequently between yucca plants, so that there may be considerable geitonogamy (which may partially account for the low proportion of fruit set in this genus). Also up to 70% of the female moths in a population lack the "tentacles" necessary to ball up the pollen (Davis 1967).

But the discovery that some yuccas produce nectar in measurable quantities suggests that the nonfeeding female yucca moths are not the only pollinators of the yuccas (Galil 1973).

Most interestingly, another genus of yucca moths has been discovered (Davis 1967). This is *Parategeticula pollenifera* Davis, which occurs on *Yucca schottii* Engelm. in Arizona and on *Yucca elephantipes* Regel in Vera Cruz, Mexico. Undoubtedly, it will be found elsewhere in the future.

Parategeticula pollenifera collects pollen and probably uses it in the characteristic yucca moth pattern of pollinating the stigma but it does not oviposit in the ovary of the flower (Davis 1967; Powell 1985) but lays its eggs in shallow pits

that it makes, usually in the pedicel of the flower (although sometimes on a petal). The larvae that hatch out migrate to the developing capsule and bore their way into it to feed (Powell 1985).

It seems that the oft-quoted obligate mutualism between yucca moths and yucca plants is going to be revealed to be a considerably more complicated story than has been handed down in the textbooks for about a century.

Sex-lability.—Dioecious and monoecious flowering plant taxa are generally thought of as having stable “sex-determination” in their flowers, but sex-lability may be of more frequent occurrence than we thought likely only a few years ago (Freeman, Harper and Charnov 1980, Freeman, McArthur, Harper and Blauer 1981). There are plants that change sex on a size basis, e.g., *Arisaema* (Policansky 1981) on a sequential basis, e.g., *Aralia hispida* Vent. (Thomson and Barrett 1981; Barrett 1984), or on an environmental basis, e.g., *Cynoches* and *Catasetum* (Gregg 1976) (usually with stressful conditions signalling a pollen production response and more favorable conditions being utilized for seed production). A similar result may be achieved by selection of either staminate or pistillate plants that are themselves seasonally stable but adapted to different niches (Freeman, Klikoff and Harper 1976; 1980; Cox 1981). This has been studied in temperate and tropical habitats and I believe will be found more often in the future.

The immense pollen production of wind-pollinated species has been logically explained as a measure of the random dispersal of the pollen and the subsequent likelihood that by far the greater amount of pollen will fail to find its way to a receptive stigma (e.g., Jaeger 1961). But the work started by Niklas on the aerodynamics of pollen borne by the wind (gymnosperms, Niklas 1984; angiosperms, Niklas and Buchmann 1985) and the structure of the cone or flower shows that the morphology of the receptive organ may assist in channeling some of this pollen to the right place—the ovule or the stigma respectively. Clearly there will be more work on this subject in the future.

NEWER TOPICS OF INVESTIGATION

Nectar and pollination.—Considerable attention is being paid (particularly by my wife and myself) to the chemistry of nectar in relation to pollinator-service and to phylogeny (e.g., Baker and Baker 1975, 1976, 1982, 1983; Baker 1976). Also see Scogin (1984, 1985).

Relatively old is the realization that nectar sugar composition and concentration, as well as amino acid composition and concentration, may be correlated with pollinator type and have strong phylogenetic connotations (Baker and Baker 1976, 1982). There is no need for a long list of our findings and those of others but we can simply refer to a clear-cut case of the value of this kind of study—our investigation of the correlation of nectar parameters and pollinatory biology of species of the largely tropical tree genus *Erythrina* (Baker and Baker 1979, 1982, 1983).

In the genus *Erythrina* there is a striking difference in the morphology of the flowers and the inflorescence in which they are borne between those species that are pollinated by passerine (perching) birds and those serviced by hummingbirds. This was first noticed 48 years ago by Van der Pijl (1937). The flowers of the passerine bird species (Fig. 1) are twisted so that they face back to the peduncle

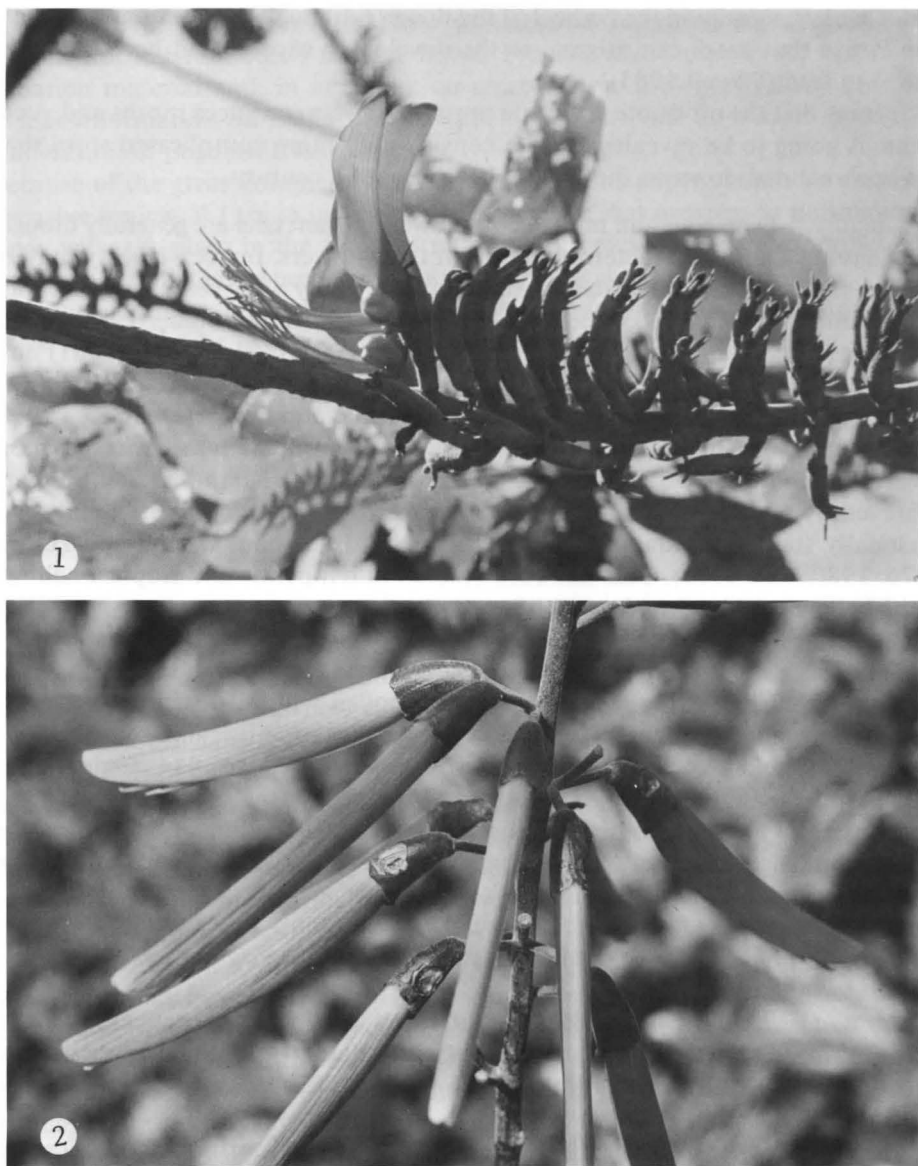


Fig. 1-2. 1. Inflorescence of *Erythrina perrieri* R. Viguier representing the passerine-bird pollinated species of this genus. Note the "gaping" flowers twisted through 180° to face the peduncle where the birds stand. ($\frac{3}{4}$ natural size.)—2. Inflorescence of *E. amazonica* Krukoff representing the hummingbird-pollinated species. Note the tubular flower standing out from the peduncle, accessible to hovering birds. (Natural size.)

on which the nectar-seeking bird stands. They gape open. This pattern is shown by trees in the Old World and the New World. In the hummingbird flowers (Fig. 2), the corolla is tubular and points out from the inflorescence so that it is easily available to hovering hummingbirds, which are, of course, restricted to the New World.

There is one species that is common to the New World and the Old World—*Erythrina fusca* Lour., and the evolutionary pattern is best explained by the origin of the genus in the Old World and its spread to the New World, where it encountered hummingbirds and radiated under the influence of these birds as well as developing some more passerine bird-pollinated species.

What is chemically interesting is that all the passerine bird-pollinated species have low sugar content in freshly produced nectar (ca. 7–16%) while the hummingbird species have more concentrated sugars in the nectar (up to 38%) (Baker and Baker 1979, 1982, 1983). Conversely, the nectars in the passerine bird-pollinated species of *Erythrina* have a much higher amino acid concentration than the nectars of hummingbird-pollinated species (Baker and Baker 1982, 1983).

The nectars of the passerine bird-pollinated species are hexose dominant while the nectars of the hummingbird-pollinated species are sucrose rich or sucrose dominated. This chemical distinction between the sugars of passerine bird-flower nectars and hummingbird-flower nectars is also true of bird flowers of other families and this generalization needs functional explanation (Baker and Baker 1983). We are working on it.

Incidentally, the inheritance of the amino acid complements of the nectar of two species when they are crossed is additive in the F_1 . This can be useful in discovering the parents of allopolyploids (Baker and Baker 1976).

There are other aspects of nectar chemistry that we aim to cover in the future. One of these is the cause, taxonomical distribution, and adaptive significance, if any, of the very wide range of pH's in floral nectars. Thus, species of *Oxalis* may have a nectar pH as low as 1.6, whereas, at the other extreme, *Viburnum costaricanum* Hemsl. has nectar whose pH has been measured at about 10 (Baker and Baker unpub.). However, most nectars have pH's in the vicinity of 5.6 to 5.9. We have evidence that oxalic acid contributes to the extreme acidity of the *Oxalis* nectar, but the broad picture of nectar pH and any correlation with pollinator type remain to be established.

The distribution and concentrations of other nectar chemicals, such as lipids, phenolics, alkaloids, and nonprotein amino acids remain to be investigated. One particularly intriguing problem concerns the melanin-containing black nectar which is abundantly produced by *Melianthus* species in South Africa (first described by Scott-Elliot 1890). It is taken by sunbirds—but why does it have to be black?

Stefan Vogel drew our attention to lipids that almost completely replace the sugars as major constituents of the nectars of certain taxa (mostly tropical, including especially the family Malpighiaceae) (Vogel 1974). They seem to have a very real function in nest provisioning by the bees (particularly of the genus *Centris*) that pollinate these plants.

And recently, Armbruster (1984) has shown that neotropical species of *Dalechampia* (Euphorbiaceae) produce floral resins that are collected by bees. *Clusia* (Guttiferae) flowers also provide resins for nest building and, at the Pacific Tropical Botanical Garden, in Hawaii, we recently saw honey bees collecting the resins of *Clusia rosea* Jacq. flowers so avidly that they could not be disturbed by our investigation. Much more remains to be done in regard to these chemicals.

Instrumentation.—Another area in which new investigations are possible is the use of more instrumentation—whether this be night-viewing devices, or reflec-

tance spectrophotometers for the better understanding of flower color as these may be seen by the eyes of a flower visitor rather than by us.

The highly technical aspect of the "neutron activation" method of analyzing the dispersal of pollen between flowers developed by Handel (1976, 1983) may make the old technologies of putting colored or fluorescent dyes in the stamens outdated—as long as the radiology laboratory facilities that are required are available.

Pollination ecotypes.—One aspect of pollination biology that does not require high technology but, instead, a willingness to spend time in the field making observations of pollinators, is the variation in pollinators that may be found in different parts of the distribution of a wide-ranging flowering plant species. The existence of what we may call "pollination ecotypes" was first put forward by Verne and Karen Grant (1965), in the case of *Gilia splendens* Dougl. ex. Lindl. (Polemoniaceae). This southern California species is generally pollinated by a long-tongued bee-fly, *Bombylius lancifer* Osten Sacken, but in the San Gabriel Mountains another fly, *Eulonchus smaragdinus* Gerstaecker, is the most frequent visitor. In the San Bernadino Mountains a stouter corolla tube lends itself to hummingbird pollination by *Stellula calliope* Gould, while on the fringe of the Mojave Desert a small-flowered form is autogamous.

Gordon Uno (1979) has studied the reproductive biology of *Iris douglasiana* Herb. in northern California. Here there are two distinct races of the species. On the coastal prairie there grows a deep bluish purple form, while in the redwood and mixed evergreen forest there is a creamy white form. The flowers of the coastal form are smaller than those of the forest form and they are more tightly attached to their pedicels (characters that help them stand up to strong winds, which are frequent). They bloom from February to May compared with April to June for the forest form. They produce abundant nectar, which is collected by a pair of bumble bee (*Bombus*) species and another bee of the genus *Emphoropsis*.

By contrast, the white-flower form, which shows up more clearly in dim light of the forest, produces less nectar but more pollen. It is visited by pollen-collecting *Andrena* and *Lasioglossum* bees and nectar-collecting *Eulonchus* flies. Another species of *Bombus* is also an occasional nectar collector in the forest. These "pollination ecotypes" show some evidences of hybridization where they come into contact, as would be expected of intraspecific ecotypes.

Working with *Polemonium viscosum* Nutt. in the Colorado Rockies, Galen (1985) has shown altitudinal differentiation in pollinator attraction. At lower elevations where flies are more common than bumble bees, the former are responsible for more seed setting. This was correlated with a greater proportion of "skunky smelling" plants at this elevation. At higher elevations, where the bumble bees are more common, more seed was set by sweet-smelling flowers than skunky ones.

Within-plant changes.—Adaptation to more than one kind of pollinator can also occur even in one plant (usually with temporal separation of the visits by the alternates). Thus, in Costa Rica, Salas (1974) showed that the tree *Inga vera* Willd. subsp. *spuria* (Willd.) J. Leon is visited in the late afternoon (when the flowers open) by lepidoptera and hummingbirds. The nectar is sucrose rich (Baker and Baker 1983), which is appropriate for these visitors. But, at night, there appears

to be hydrolysis of the sucrose and, accompanied by the development of a sour smell, a hexose-rich nectar is available and appropriate to the bats that visit the inflorescences then.

These are daily variations; a most interesting case on a *seasonal* basis has been described recently by Paige and Whitham (1985) in *Ipomopsis aggregata* (Pursh) V. Grant (or *Gilia aggregata* [Pursh] V. Grant, as you like).

This species, which has been much used in pollination studies, has populations in northern Arizona containing flowers of various shades of red or white. The red flowers are appropriate to hummingbirds, which are important pollinators over most of the blooming season (beginning in early to mid-July).

But with emigration of one of the two hummingbird species in mid- to late August, the hawkmoth, *Hyles lineata* (Fabricius) becomes proportionately more important as a pollinator and there is a change of flower color to pink or white, both in terms of individual inflorescences and of newly flowering plants. Percentage fruit setting at this time is greater in the color-adapted plants than in those with simply red flowers.

It remains to be seen if this is a unique case or whether other examples of change in adaptation to pollinators on a seasonal basis can be found.

More modest color changes are common in the petals (as in the rosy flush that develops during the day in flowers of *Gossypium*). Similarly, changes in the color of nectar guides, such as those to be seen in *Aesculus hippocastanum* L. (which change from yellow to red) as the flowers age (illustrated by Jaeger 1961), may have adaptive significance in cutting down useless pollinator visits, leaving the pollinators time and energy to concentrate on the fresher flowers. Further quantitative studies are indicated.

Phylogenetic constraint.—Close adaptation to more than one kind of pollinator, or even to only one pollinator, may not be freely attained—for there is always “phylogenetic constraint” to be contended with. This is the restriction on present adaptation that is imposed by the inheritance of genes that are “fixed” in the genome for certain characteristics.

An illustration of this is provided by the African baobab, *Adansonia digitata* L., which belongs to the Bombacaceae. This is a family in the Order Malvales in which a single style is apparently an invariable character. Elsewhere in the Malvales, in a *Hibiscus* flower for example, the stigma is likely to be touched by any large flower visitor that comes along. In *Adansonia* (Fig. 3) the ball of stamens will be contacted every time by the bats that visit the flowers and take nectar from the base (uppermost) of the flower, but only when they happen to come in at the side where the style protrudes will they deposit pollen on the stigma. The ideal would be multiple styles arranged like the spokes of a wheel.

But the baobab, even with this maladaptation, is successful as a savannah tree in Africa, probably because it lives to a great age and does not depend upon a high percentage of fruit and seed setting.

Molecular genetics.—On the subject of genetical organization, the findings of modern molecular genetics must be taken into account. Instead of unflinching stability, the genome appears to be in a dynamic state. Transposition of genes between nonhomologous chromosomes can take place (see any up-to-date molecular biology book) and the resulting inheritance may be subjected to selective

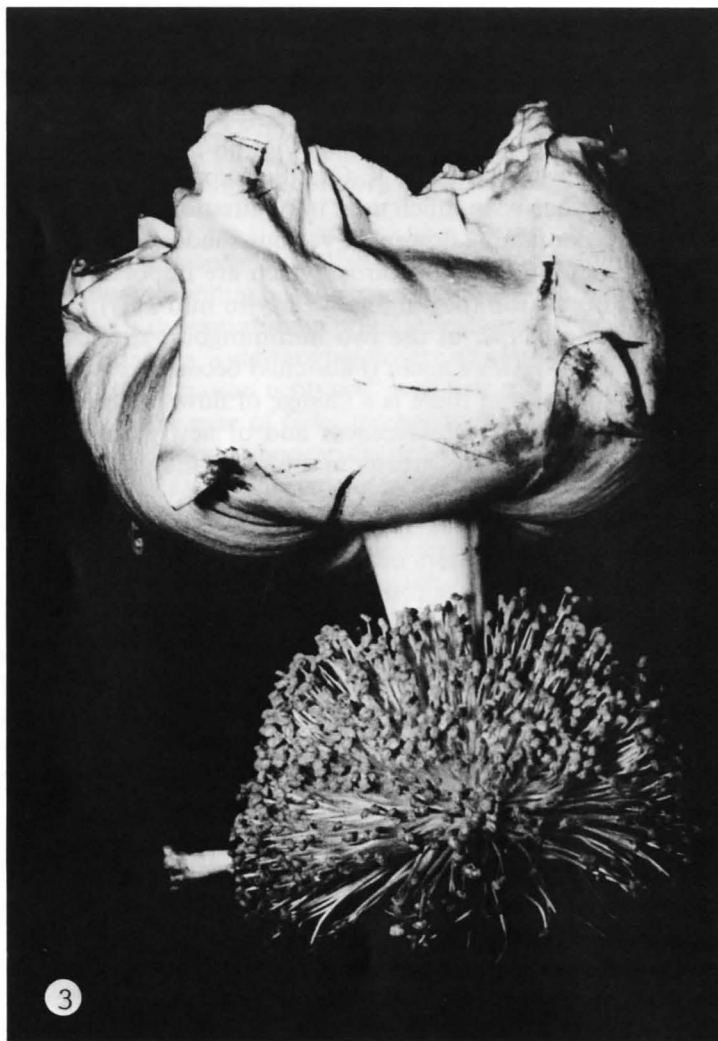


Fig. 3. Flower of *Adansonia digitata* in Ghana. Note claw marks of bats on the reflexed petals, the ball of stamens and the single style projecting from it. (Natural size.)

pressures. We can no longer be sure that a clone or even an old tree is entirely genetically uniform.

But conversely, this movement of genes around the genome may be important in assembling, with close linkage, genes that will control several developmentally and functionally important characters. This may have been the way that the "supergenes" that control the syndrome of morphological and physiological characters that are to be seen in cases of heterostyly came into existence.

Collaboration.—Of course, there will be integration of pollinatory biology with other disciplines; for example, there will be collaboration with chemists on the chemistry of scents (of nectar and pollen, as well as elsewhere in the flowers).

There will also be collaboration with physicists on such items as color perception by flower visitors and the electrostatics of pollen/stigma relations that have been pointed out by Erickson and Buchmann (1983).

But within biology there will be increased interdisciplinary interaction on the behavior of anthophilous animals; several studies of the influence of nectar chemicals on insect or vertebrate pollinator behavior have already been made. Hainsworth and Wolf (1976) have tested amino acids added to sugar water on the behavior of hummingbirds. Inouye and Waller (1984) have done the same for honey bees. Janet Lanza (pers. comm.) has begun investigations of a related subject, the influence of amino acids on the behavior of ants that normally go to extrafloral nectaries. All agree that amino acids have effects on behavior but the effects seem to vary enormously. Collaboration with Oliver Pearson is providing research results on the rate of passage of sugar solution through the guts of hummingbirds in relation to the apparent preference of these birds for sucrose-rich nectars (Stiles 1976; Baker and Baker 1983).

Studies such as these and the pioneer work on pollinator energetics by Bernd Heinrich (especially with bumble bees) show the way that experiments may be increasingly used to supplement field observations (Heinrich 1983a).

Most of these considerations of the mutual influences of plants and pollinators tend to be one-on-one situations, but to be realistic these events must be put in a natural context. We may expect to see the development of such studies in the future. Population studies are the next step in organization and the new books listed at the beginning of this paper have many contributions that point the way.

FERTILIZATION AND SEED DEVELOPMENT

A logical outcome of successful pollination is fertilization and seed development. Although this may not be a part of pollination biology in the strict sense, it is so intimately connected that some attention must be given to it. The breeding systems of the plants—dioecism, monoecism, hermaphroditism, dichogamy, and the incompatibility systems—all play a role in the reproductive biology of seed plants and will continue to be studied with profit (Willson 1983; Stephenson and Bertin 1983).

Low seed set may be due to inadequate pollination (which can only be ascertained in the field) or to failure of pollen tube growth, failure of fertilization, or failure of endosperm or embryo development, or to fruit abortion (Stephenson 1981). Such discriminating influences are assumed to proceed selectively with "higher quality" seeds maturing and "lower quality" seeds not being formed or matured. "Quality" is usually not defined (see review by Willson 1983).

But there is little hard evidence in the studies made so far for the selection of physiologically superior offspring by directing foodstuffs to the development of the favored embryos, and it must be remembered that even vigorously growing embryos are not necessarily fitter than more modestly growing progeny that have more appropriate adaptation to the environments in which the plant flourishes or could flourish.

What is certain is that hermaphrodite flowers produced after enough embryos are formed in that inflorescence may still be parentally active through the pollen

they produce and disperse (e.g., *Catalpa speciosa* Warder, Stephenson 1981). Also see Lloyd (1974).

POPULATION AND COMMUNITY PHENOMENA

A thought-provoking contribution from Price and Waser (1979; also see Waser and Price 1983) is their demonstration in *Delphinium nelsonii* Greene that there is an optimum distance from which pollen should be recruited to give vigorous and well-adapted progeny. Plants growing too close to the receiver will probably be ancestrally closely related and the progeny may show inbreeding depression even if there is not sheer incompatibility. Plants growing farther away may be adapted to a different microhabitat, and pollination from this may result in imperfectly adapted plants. Nevertheless, it seems that pollination under natural conditions is most often from pollen sources closer to the recipient than the "optimal" distance. See also Levin (1984).

In her study of trees of the genus *Inga* in Costa Rica, Koptur (1984) found only evidence of short-distance ineffectiveness of pollination as far as seed production is concerned. Understandably she did not raise subsequent generations of these trees.

This phenomenon may be expected more likely to be shown by species inhabiting closed climax communities rather than opportunistic colonizers.

Mary Willson (1979) and Stephenson and Bertin (1983) have reviewed the subject of sexual selection in detail.

Increased attention will surely be given to the behavior of potential pollinators as they forage on inflorescences and between plants. "Optimal foraging" (that produces maximum fitness of the forager by the most efficient pattern of reward collection) (Pyke, Pulliam and Charnov 1977; Waddington and Horden 1979; Pyke 1984) may be an ideal but it seems that the natural picture is one of less than complete agreement with the postulates. Bernd Heinrich (1983b) has stressed the inadequacies of strictly "optimal foraging" as a basic principle of pollinator behavior. Predation and innate behavioral patterning may interfere with the optimum. Some nectar and pollen collectors are easily diverted from a flower—and some are victimized (deceived) by the plants or even temporarily imprisoned. The water lilies, *Nymphaea* species, are lethal to the bees they attract (Meeuse and Morris 1984).

Intrapopulation variation in nectar production of *Heliconia* species in Trinidad has been shown by Feinsinger to be an effective economy. The pollinators continued to be attracted by the "bonanza" flowers while energy was saved by the "blanks" (Feinsinger 1983).

Several aspects of coexistence in ecosystems need consideration. This is particularly well treated in Section VII of the "Handbook of Experimental Pollination Biology" edited by Jones and Little (1983).

Flower color.—Some synoptic studies of natural communities have been concerned with flower colors since Hermann Müller made quantitative observations in the European Alps. For example he showed that pink flowers, associated particularly with butterfly pollination, appeared to be more common in montane habitats (Müller 1883).

Kent Ostler and Kim Harper (1978), in Utah, have studied the plant com-

munities of the Wasatch Mountains and found that the least diverse communities are dominated by yellow flowers, but with increased diversity, blue flowers, associated with specialist pollinators, become more important.

Observations of my own on flower color in Marin County, California (Baker unpub.), showed 45% of the species in open grassland to have yellow flowers, whereas 91% of the herbaceous species in the coast redwood forest have white or pale pink flowers. Purple flower color was best represented at the forest margins.

Karen and Verne Grant (1968) have developed the postulate that pure red flower color, so characteristic of hummingbird-pollinated flowers in western North America, is a highly visible signal to a migrating hummingbird that there is a nectar reward awaiting it—a signal that supposedly cannot be seen by bees. Hummingbirds can be trained to visit any color but there are advantages to red—apart from its invisibility to bees. The red flowers show up clearly on a green background, especially in the reddish light of dawn and dusk, when hummingbirds forage vigorously (Baker 1961). However, it does not seem necessary to restrict this signalling theory just to migrant-bird attraction. Pollinator sharing can take place in certain circumstances where the flower visitors are not migrating.

Pollinator sharing.—Pollinator sharing may result in mutualism or competition between plants depending upon the circumstances. In some cases (e.g., in densely packed stands of annual plants in the California grasslands) there will be competition between plants for pollinators and in other cases (e.g., coastal forests and marshes in British Columbia in late summer [Pojar 1973]) the situation will be reversed. The former seems to be the case more often in ecosystems ranging from Arctic tundra (Hocking 1968) to the wooded tropics (Heithaus 1974, 1979).

Pollinator sharing by members of the same genus with consequent similarity of flower morphology, color, and behavior can be successful if there is phenological separation of the species as Flemming (1985) found in five sympatric species of *Piper*. This may be the result of in situ natural selection of complementary flowering times as Stiles (1977, 1978) has suggested for hummingbird pollinated species of *Heliconia* in Costa Rica, or, as Poole and Rathcke (1979) have contended, it may be a random distribution of flowering times that were not adjusted in situ. In either case, the phenological differences are probably effective in cutting down interspecific pollen flow while keeping the pollinators in the area.

Donna Howell (1977) has given evidence that unrelated woody plant species may share pollination by bats in Costa Rica by concentrating their reward production at different times of the night and by positioning the pollen on different parts of the bat's body.

Where pollinator sharing is between species that flower at seasonally distinct times, there may be carry-over influences as Waser and Real (1979) have shown for the sequentially blooming *Delphinium nelsonii* and *Ipomopsis aggregata* in the Rocky Mountains near Crested Butte; a poor flowering by the *Delphinium* reduces the availability of hummingbirds to the usually later-flowering *Ipomopsis*.

James Brown and Astrid Kodric-Brown (1979) have suggested that competition for pollinators may be a weak force in the evolution and ecology of pollination systems. This fits with the revelation that adaptation to different pollinators by *Aquilegia* species in the high montane areas of the Sierra Nevada is far from complete (Grant 1952, 1976; Chase and Raven 1975). Hummingbird-pollinated

Aquilegia formosa Fisch. in DC. and hawkmoth-pollinated *A. pubescens* Cov. hybridize (probably under the influence of big bees) and their ecological separation to coniferous forest and tundra, respectively, has been a stronger force in keeping these taxa more or less intact (Chase and Raven 1975).

There must be much more study of this kind of interactive pollination biology.

Mimicry.—Linked with these matters is the degree of similarity in morphology, color, scent, and rewards that is shown by the sharers. Mimicry has been a favorite topic for pollination biologists, ranging from the pseudocopulation of insects with orchid flowers to the much more prosaic subject to which southern California investigators have contributed worthily.

John Little (1983) and Paulette Bierzychudek (1981) at the Rancho Santa Ana Botanic Garden as well as Elizabeth Powell and Eugene Jones (1983) from neighboring Fullerton, have made observations and conducted experiments that show some but not all mimicry to be real. Amots Dafni (1984), has reviewed the subject very recently and I need not go into detail. But I must emphasize that when we investigate flower mimicry we have to put aside our own visual appreciation and take a view more like that of the agent that is being exploited by the mimic.

This is beautifully demonstrated by the observation by Nilsson (1983) that blue-flowered *Campanula rotundifolia* L. and *C. persicifolia* L. and the bright reddish-purple-flowered orchid *Cephalanthera rubra* L. C. Rich. share the same species of solitary bee (*Chelostoma fuliginosus* [Pz.]) in Sweden. The orchid produces no nectar and its pollen is not collectible for use by the bee nutritionally, being bound in pollinia. The male bees take nectar from *Campanula* and the female bees collect nectar and pollen from the *Campanula*. But the males emerge as much as two weeks before the females bees, and during this period of time they are lured to the orchid flowers while they patrol looking for females. *Cephalanthera rubra* does not set seed in the absence of *Campanula*.

This is reminiscent of the phenology of the other hymenoptera, those that indulge in pseudocopulation with orchids (Kullenberg 1950; Kullenberg and Bergstrom 1976).

At first sight it would seem that the morphology of the flowers and particularly flower color are so different in *Campanula* and *Cephalanthera* that neither one could be a mimic of the other. But a spectrophotometric analysis of the flower color, at least, shows that with the exception of the red component (around 650 nm) in *Cephalanthera* (which the bees cannot see) the spectrographs are remarkably similar.

This must also make us careful about what seem to be possible cases of mimicry to the human eye. Also there must be a positive influence on the fitness of the mimic. The absence of demonstrable increase in seed-setting by the mimic may justify Bierzychudek's (1981) distrust of a mimicry interpretation of the classic case of apparent freeloading that is represented by nectar-producing *Lantana camara* L. (Verbenaceae) and *Asclepias curassavica* L. (Asclepiadaceae) and the nectarless *Epidendrum radicans* Pav. (Orchidaceae) in Central America.

William Haber (1984), working in Costa Rica, at Monteverde, shows that the frangipani, *Plumeria rubra* L. (Apocynaceae), has an almost complete syndrome of characters adapting it to cross-pollination by hawkmoths and, indeed, the flowers are freely visited by 17 species of hawkmoths. Despite this, *P. rubra* does not produce nectar and it may be regarded as a deceptive mimic of a generalized

hawkmoth-pollinated model. The odd thing is that it is more abundant than any individual species of the nectar-producing models. However, its fruiting rate is very low (less than 0.1%) even though it appears to be self-compatible.

An aspect of mimicry that future investigations may show to be very important, particularly in the tropics, is the mimicry of staminate flowers by pistillate flowers in dioecious and monoecious species (Baker 1976; Bawa 1980). We are used to seeing strong differentiation between the pollen dispersing and accepting flowers of wind-pollinated dioecious and monoecious trees in temperate regions, making the system more efficient in using this abiotic pollen vector. But in the prevalent animal pollination situation in the forested tropics it is essential that the biotic pollen vector be attracted to both staminate and pistillate flowers, so the physical resemblance between the two kinds of flower is strengthened by staminode development in pistillate flowers or other means of maintaining what will be a "search image" by the pollinator.

It is probably for this reason that taxonomists have also been misled by the similarity of the sexes and have described taxa as being hermaphrodite instead of monoecious or dioecious (Styles 1972).

ECOSYSTEM STUDIES

True ecosystem studies in pollination biology have scarcely been attempted probably because of the immensity of the task. A graduate student at Berkeley, Paul Cylinder, is showing how the task may be approached in stages. In a subalpine meadow in the Sierra Nevada he is studying the pollination biology of a "guild" of flower visitors which visit the larger-flowered, taller herbaceous species for nectar. This guild is made up of bumblebees, butterflies, and hummingbirds. The small-flowered plants in the meadow are usually of short stature and probably largely self-pollinated. They can be studied next. Then there will be the wind-pollinated species. These also can be studied in the future, so that ultimately a complete picture for this relatively compact ecosystem can be drawn.

Pamela Yorks (1980) has followed the nectar availability and constitution over the whole flowering season in a chaparral/mixed evergreen forest in the East Bay hills.

The work of many investigators in the vicinity of the Rocky Mountain Biological Station, near Crested Butte, Colorado, is also providing researchers there with information from which a complex local picture can ultimately be synthesized. This pattern of building on the studies of other workers is an advantage provided by the existence of research stations. Not only can there be joint investigation by specialists but also there is built up a continuously increasing (progressively more valuable) compendium of information about the ecosystem adjacent to the station.

In the tropics, e.g., La Selva, Finca "La Pacifica" and the Forest reserves at Santa Rosa and Monteverde, all in Costa Rica, will become ever more important as base line information is accumulated by the sequence of researchers who use these stations. The Smithsonian Tropical Institute on Barro Colorado Island, Panama, is invaluable as a locale for reproductive biology research for the same reasons.

But I reiterate my belief that interested persons without large grants for equipment and travel can perform satisfying research on this subject, from which we anticipate significant evolutionary revelation.

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FOOTNOTE

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